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The minds of insects

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Andy Clark's philosophical thought and writing run in a strangely parallel course to my own research. On the face of it, our topics and approaches have little in common. I work on insects and robots: trying to build detailed, plausible models of the physical and neural mechanisms underlying specific behaviours, such as how crickets detect the wind front created by a predator strike and take rapid evasive action (Webb 2002), or how the spring-and-damper mechanics of the body segments of maggots can give rise to coordinated peristalsis with only local feedback (Ross et al. 2015). Meanwhile Clark has sought to develop a unified vision of how cognitive, potentially conscious, creatures such as ourselves 'get a grip' on the world, masterfully drawing together a wide range of philosophical, psychological and neuroscientific insights (Clark & Grush 1999; Clark & Chalmers 1998; Clark 1997; Clark 2013). Nevertheless, our paths continue to cross¹, in sometimes surprising, and I hope productive, ways.

In particular, as I will try to illustrate in the remainder of this chapter, the insect systems I study can provide useful 'edge cases' against which to test any supposedly general, or "truly unifying account of perception, cognition and action" (Clark 2015, p.2). Indeed it is still a subject of sharp debate whether the term cognition should be applied to insects at all (Menzel & Giurfa 2006; Giurfa 2013; Webb 2012), although it is hard to deny that many of the key examples discussed by Clark in the context of human behaviour have close parallels in insect capabilities. The dragonfly easily outperforms most baseball fielders in their ability to intercept a small moving target (Mischiati et al. 2014). Bees have a spatial memory flexible enough to incorporate information about far distant food sources they have gained from another bee's dance communication into their own experience, so as to take novel short cuts (Menzel et al. 2011). Leaf cutter ants extend their behavioural repertoire by building complex nest structures surrounded by foraging highways, which supports 'farming' of a symbiotic fungus, including temperature regulation through turret construction (Cosarinsky & Rocas 2012). Yet it seems the "brain" envisioned by Clark in much of his writing is exclusively a mammalian one, with the cortex the key structure on which to ground theoretical concepts such as predictive processing.

If we can extend the same explanations, as well as grant at least some of the same capacities, to insects, this may offer some advantages for cognitive neuroscience, i.e., understanding how brains actually implement the proposed mechanisms. Insect neural circuits are more accessible in a variety of ways: amenable to a wide variety of tools for measuring or manipulating brain activity while measuring behaviour; and on a scale that we can plausibly model at the single identified neuron level. But even at the conceptual level, insects potentially offer the nearest thing we have to an 'alien' intelligence, that is, an intelligence that emerged from an independent evolutionary pathway (assuming our pre-Cambrian common ancestor did not cognize). As such, the extent to which they have converged on the same solution(s) is clearly of interest.

To date, insects have served Clark's philosophy more as an example of embodiment than as an example of mind: illustrating the dynamic links of brain, body and environment that produce behaviour and cannot be easily decomposed into distinct sensing, planning and action processes. Thanks to Andy's promotion (Clark 2001), my earlier research on cricket phonotaxis (Webb 1994)

¹often literally, as we work in adjacent buildings

has become a popular example of the principle. To briefly recap: a female cricket can find a mate by orientating towards the song produced by a male, which seems to require filtering to recognise the species specific frequency and chirp pattern as well as determination of the sound direction (Schildberger 1988). However, solving the second problem contains at least a partial solution to the first, and moreover depends far more on the physical structure of the auditory apparatus than on internal processing. The cricket's ears are on its forelegs and are connected by a tracheal tube, forming a pressure difference receiver that is directional for sound (Boyd & Lewis 1983). The length of this tube already 'tunes' the animal to have the strongest directionality for the correct song frequency. This directionality is transduced by the cell properties of receptors and interneurons into a latency difference in firing (Pollack 1998). A simple (one neuron) comparison of latency to make the steering 'decision' to turn left or right will inherently depend on the temporal pattern. Thus the recognition problem is already solved. Implemented in a robot (Lund et al. 1997), the result is summarised in Clark (2001), p106: "understanding the behaviour of the robot cricket requires attention to details that (from the standpoint of classical cognitive science) look much more like descriptions of implementation and environmental context than substantive features of an intelligent, inner control system". Importantly, "it exploits highly efficient but (indeed, because) special purpose strategies", and "it is not at all obvious that the robot cricket uses anything worth calling internal representations".

Myriad examples of this type have influenced the 'embodied mind' debate to the following extent: it now seems hard to deny that a full understanding of cognition in an acting agent requires moving beyond representation in the head to take into consideration the dynamic brain, body and environment interaction. Whether this means the 'mind' really exists beyond the head I will leave to other authors in this volume to explore. However, it remains notable that the embodied view is not yet mainstream amongst neuroscientists, who are still inclined to view neurons firing in response to an external stimulus as constituting 'representation' of that stimulus to the animal, and the brain's principle task as decoding the signal to construct a veridical model of what is out there. Even more surprisingly, given the direct face-off with the reality of physics that robotics requires, the conventional robot engineering approach is still dominated by the assumption that obtaining an accurate internal world model is the crucial first step for any perception-action loop (the main advance is that these models are now typically expressed in a probabilistic form). But what should have been learnt from the embodiment debate is that, from the animal (or robot) point of view, successfully controlling action is rarely helped by such decoding. The system needs to transform sensory signals into motor outputs, not reconstruct an accurate representation of the causes of those signals (Webb 2006). In recent work (Clark 2015), Clark has skilfully explained how maintaining the centrality of the embodied/dynamic perspective can prevent falling into this 'reconstruction' trap, even when the brain's ability to infer and predict, indeed to represent, becomes the specific focus of enquiry.

Following on from the cricket, my research group have explored a number of other insect/robot systems that similarly exploit the interaction of physical and neural mechanisms, in entangled feedback loops. For example, the turning behaviour of a walking insect, such as the cricket, might appear to require complex coordination of the large number of degrees of freedom in six, multi-jointed legs (Petrou & Webb 2012). However it can be replicated by assuming the front legs alone target an attractive stimulus, and the mechanical linkage between the body and legs induces the appropriate motion in the remaining leg joints; as a consequence, simple local positive feedback to enhance the intrinsic motion is sufficient to replicate realistic movement patterns (Rosano & Webb 2007). For a flying insect, the problem of approaching odour sources carried on a complex, noisy wind-plume can potentially be explained by assuming odour-taxis exploits the existence of robust

visual control loops for stabilisation and collision avoidance. If changes in odour concentration are used simply to alter the gain on these control loops, enhancing the tendency to keep flying in the current direction, the odour can be localised successfully (Stewart et al. 2010). These visuo-motor loops themselves depend on ‘matched filter’ processing (Wehner 1987) with neurons wired to be responsive to highly specific global motion patterns corresponding to imminent collision (expansion) or tendency to veer from straight flight (global rotation) (Krapp & Hengstenberg 1996).

What soon became a pressing question for us in trying to unravel and model these ‘simple’ behaviours in ‘simple’ animals was how insects manage to combine these various well-tuned sensorimotor loops into overall coordinated and adaptive action. A further ‘simple’ yet revealing example arose when (inspired by behavioural experiments from (Böhm et al. 1991)) we tried to equip our phonotactic robot with a basic optomotor reflex (Webb & Harrison 2000). The optomotor reflex, found in many animals including ourselves, occurs when the entire visual field appears to be rotating in one direction, to which the animal responds with a compensatory body or eye rotation. This reflex is adaptive for stabilisation, as the likely cause of such wide-field visual motion is that the animal is (unintentionally) drifting in its heading direction, thus the reflex allows the animal to keep looking or moving in the same direction with respect to its environment despite disturbances. But ‘unintentional’ is key. Our robot, attempting to turn left towards the sound, would immediately experience a strong rightwards optomotor stimulus, causing it to make a ‘corrective’ turn right, which was great for maintaining a straight course but entirely ineffectual if trying to track down a sound source. The solution seems obvious (and indeed was suggested more than fifty years ago (von Holst & Mittelstaedt 1950)) – the robot (or insect) should anticipate the predictable visual feedback from its *intended* rotation, and internally cancel out the optomotor reflex (Webb & Reeve 2003). Yet this simple observation opened up a wide and ongoing research agenda, to understand what and how an insect brain predicts, and what role prediction plays in its successful adaptive behaviour.

Thus my work again converged with Clark’s, around the conceptual centrality of prediction for even basic sensorimotor control, and how this might provide a scaffold on which a representational cognitive system might be built. In (Clark & Grush 1999), Clark and Grush discussed this in the particular form of an ‘emulator’ or forward model: for the animal to make a prediction of expected feedback, it needs to internally emulate the external contingencies that produce this feedback. Thus “emulator circuitry would constitute the most evolutionary basic scenario in which it becomes useful to think of inner states as full blooded representations” (p.7). So perhaps the cricket has internal representations after all? In 2004, I briefly surveyed the evidence for forward models in the insect brain (Webb 2004), and this seems a useful opportunity to mention some more recent evidence.

In that article I discussed evidence from cricket auditory interneurons that, when a male is singing, an appropriately timed inhibition signal arrives to cancel out the response to each of its own chirps, allowing it to distinguish the songs of surrounding competitors. Since then, the specific neuron carrying this signal from the central pattern generator for song production to the auditory system has been identified (Poulet 2006). For the optomotor response discussed above, it has been reported in fruitflies that the key wide-field visual motion sensitive neurons involved in this reflex, the horizontal cells in the medulla, receive an internally generated input when a tethered fly attempts spontaneous turns (Kim et al. 2015). The signal is opposite in sign, and of an appropriate scale, to cancel the expected visual input of the corresponding rotation. Notably, this is not just inhibitory gating of the sensory system (which might seem too basic to require an emulator), but is directionally and temporally tuned to the expected feedback. Interestingly the authors suggest it may even play a role in causing the turn, by pre-charging the optomotor system with a phantom signal that induces a reflex response. This seems intriguingly close to the suggestion that (in general) motor control might be

obtained by the brain predicting the expected sensory consequences, stimulating reflex arcs to bring this about (Friston et al. 2010).

At the behavioural level, several studies in flying insects have shown head stabilisation against their own body manoeuvres occurs too rapidly to be caused by observing the induced visual slip, implying it is driven instead by an internal expectation. In the dragonfly, the correct movement requires compensation not only for the animal's own motion but also for the expected trajectory of the small, moving target it is attempting to intercept, to keep this within a small high resolution area of the retina. By recording head and body motion in freely flying dragonflies to controlled targets (small beads resembling flies) the two effects could be separated. Compensatory head motions are made with effectively zero time lag for constant speed prey, while unexpected changes in prey motion cause a (delayed) reaction (Mischianti et al. 2014). Recordings from neurons in the dragonfly that are specifically tuned to small moving objects also show a form of selective attention, in which the response will track one of two moving objects, maintaining focus even when the cues for saliency of the second object are increased (Wiederman & O'Carroll 2013).

A particularly interesting line of evidence comes from the consideration of associative learning mechanisms in insects. Although simple association is sometimes taken as the hallmark of non-cognitive behaviour, the current dominant theoretical model is strongly tied to the notion of prediction, specifically in the form of prediction error as the signal that modulates the formation of associations (Schultz et al. 1997; Waelti et al. 2001). That is, the brain compares expected to actual reward and uses the difference to drive learning. In insects, the architecture of the key circuits underlying associative learning are being unravelled in exquisite detail, yet the direct evidence for a prediction error encoding (as opposed to a simple reward signal) is still sparse (Hammer & Menzel 1998; Terao et al. 2015), despite models showing it can successfully account for insect behavioural data (Montague et al. 1995). I have previously argued that the insect mushroom body neuropil could be a plausible substrate for forward models in insects. This is supported by the structural resemblance of the circuitry to the cerebellum (Farris 2011), the region of the vertebrate brain for which the clearest evidence of predictive signalling to cancel expected sensory feedback has been obtained (Bell 2001). Recent work on the fruitfly has provided important new insights into this structure, which is firmly established as a key site for olfactory memory (Aso et al. 2014). These include: the random connectivity of sensory inputs to a large number of parallel cells, which appears to implement the principle of high dimensional projection and sparse representation found in the support vector machine learning formalism (Huerta et al. 2004); a small number of output cells from this parallel structure, which if activated produce approach or avoidance behaviour, and whose response to a stimulus is altered after the stimulus has been paired with reward and punishment; a hierarchical structure within this set of output neurons; identification of dopaminergic neurons whose activation can substitute for reinforcement; substantial feedback connections from the output neurons to the dopaminergic neurons and to the input areas (Aso et al. 2014). The latter provides an obvious route by which prediction of reward could be conveyed, and prediction error calculated through inhibition. However as yet, proof of this function is elusive.

The mushroom body is not the only insect brain structure implicated in learning. For example, a striking behaviour that has been demonstrated in cockroaches (Mizunami et al. 1998), crickets (Wessnitzer et al. 2008) and fruitflies (Foucaud et al. 2010) is a 'place memory' capacity equivalent to rats in the famous Morris water maze. In this paradigm, the rat learns to relocate a platform concealed in an opaque pool of water, quickly learning to search in the position indicated by distal visual cues. Insects are similarly challenged by being exposed to a hot floor on which they must locate an unmarked cool spot to obtain respite. After only a few trials, they can also relocate this position from

a novel, arbitrary, starting position and will search for it (when missing) at the appropriate location relative to surrounding visual stimuli. Using neurogenetic methods to block activity in specific brain regions, it was found (in fruitflies) that mushroom body manipulation did not diminish performance, but the behaviour was dependent on a particular area of the central complex (Ofstad et al. 2011). As its name suggests, this is a centrally located neuropil in the insect brain that receives convergent input from many sensory processing areas, and has significant output to pre-motor areas (as well as feedback to sensory areas). The neuropil itself has a strikingly ordered architecture that includes multiple feedback loops. A further connection of this area to rat navigation has been provided by the demonstration that a (literal) ring of neurons in the lower part of this structure displays an activity bump that tracks the orientation of the fly relative to its surroundings (Seelig & Jayaraman 2015), in a manner highly reminiscent of theoretical models of rat ‘head direction’ cells (Zhang 1996). In particular, the activity bump persists when visual cues disappear, and will track the spontaneous turns made by the fly in darkness. As yet it is not clear if the latter effect is due to proprioceptive inputs, or could in fact be another example of internal prediction at work.

This brings me to a third crossing point with Clark’s philosophical output, as encapsulated in his most recent book, ‘Surfing Uncertainty’. The core concept of ‘predictive processing’ (henceforth PP) Clark develops there goes beyond the argument that cognition involves internal signalling of expectations (which I have suggested applies equally to insects). In addition, Clark argues, the form of this prediction is a rich cascade of probabilistic generative models. Thus representation of the uncertainty of predictions, and applying Bayesian reasoning to deal with uncertainty, is at the heart of this account (as it has been in striking recent breakthroughs in AI, e.g. deep learning). Does the Bayesian account of human brains and cognition potentially extend to insects? So far, probabilistic processing in the insect brain is not supported by any neuroscientific results of which I am aware, and even for vertebrates, the neural evidence remains nebulous. As an alternative strategy, we could consider whether the kinds of behavioural evidence for probabilistic sensorimotor processing in humans have any parallels in insects.

Perhaps the strongest line of evidence comes from the ‘optimal cue integration’ paradigm, which also conveniently lends itself to investigation in animal systems. This paradigm sets up a situation where a judgement about some property in the world – such as the size of an object – is made by an experimental subject based on several independent sensory cues – such as visual and haptic information. If the cues provide somewhat conflicting values, humans will make a judgement that combines the cues with weights proportional to their reliability, for example, trusting visual information less as noise is added to the image (Ernst & Banks 2002). Strikingly, these judgements appear to be in close quantitative match to the probabilistic optimum predicted by Bayes theorem, and multiple demonstrations of this general effect under a wide variety of situations are taken to be strong evidence that the brain must somehow encode the probability densities needed for Bayesian calculation, or (more realistically) a good approximation of it (Knill & Pouget 2004).

We have recently carried out a behavioural experiment of exactly this form on ants (Wystrach et al. 2015). Many species of ants are capable of impressive navigation without chemical trails, exploiting a range of cues that include path integration based on a sky compass and visual memory for guidance by surrounding scenery (Wehner 2008). These capabilities are already interesting from a cognitive perspective: the ant’s nest is a small hole in the ground that cannot be perceived beyond a few centimetres but the ant keeps ‘mental’ track of the direction and distance of its nest, constantly updating its home vector according to its own movement. Keeping mental track of an object in the world while out of direct contact with it is arguably a hallmark of ‘truly representational’ processing. For the current discussion, however, the main interest is that the multiple navigational mechanisms

used by the ant allow us to set up a cue conflict situation. An ant that has travelled outward and built up a home vector can be moved by the experimenter to a location where the visual memory cues indicate a conflicting direction in which to run home. Conveniently, some very general mathematical assumptions about how path integration error must accumulate for any animal with an external compass reference allow us to directly quantify the uncertainty associated with outward runs of different lengths. We found that the ants' directional choices were a compromise between the two cues, with the relative weighting changing with the path length precisely as predicted by optimal Bayesian integration (Wystrach et al. 2015).

So does this demonstrate that insect brains are doing probabilistic encoding? One additional experiment cast some doubt. We had used the outward path length to calculate the (Bayesian) weighting, but as the ants had run fairly straight, their home vector would have approximately the same length. Perhaps they could use home vector length as a 'proxy' for the actual uncertainty accumulated on the outward path, and hence the appropriate weighting to give to the home vector direction relative to visual memory? A direct way to test this was to uncouple the actual uncertainty of the path integrator, which depends on the total length of the outward route, from the home vector length, which depends on the straight-line distance home. By making ants run around in a fixed area for some time before release, the first should increase while the latter remains the same. We found that these ants took a homewards direction identical to those who had not experienced the added uncertainty, suggesting their weighting of the conflicting cues was unchanged, and supporting the proxy argument (Wystrach et al. 2015). Rather surprisingly, we also found that few studies of optimal cue integration in humans had controlled for the possibility that a proxy for uncertainty could drive the weighting, e.g., that decreasing visual contrast could be the direct cue driving a differential contribution of visual information to a decision. The proxy explanation is still non-trivial – e.g. the Bayesian weighting fits the behavioural results much better than a simple linear scaling of the weight with the cue of interest, for both ant and human data. Nevertheless, it seems plausible that the shape of the function to map from the proxy cue to the weighting (removing any need to encode probability densities) could be acquired, either through experience, or through evolution. The latter seems more plausible for the ant, as it is unlikely any individual ant gains enough experience during its lifetime to accurately tune such a function.

This outcome, if our interpretation of the results is correct, raises a serious issue. If the ant's ability to do optimal cue integration has been hard coded by evolution, does it still count as evidence for the PP view? It is clear that some supporters of this view, most notably Friston, would argue that it does: that indeed, not only innate behaviours but the innate physical structure of an animal represents a prediction of the interactions with the world it is likely to experience, acquired and tuned over time by the experiences of its ancestors. To give another example from ants: their eyes are sensitive to ultraviolet light, which enhances sky/ground contrast; such images can be stored as visual memories and used to recognise familiar locations; and the certainty of localisation can be shown to be substantially improved as a result (Stone et al. 2014). So the peripheral filtering for ultraviolet could be said to be as much an example of the predictive principle at work as any hypothetical internal use of the resulting certainty to balance the influence of visual memory against path integration. Indeed, Friston would argue that even the single celled organism's adaptive fit to its niche falls within the PP (or 'free energy') explanatory scope.

However, in 'Surfing Uncertainty' (2015) Clark departs company with Friston at these more extreme examples, preferring to use scare quotes for 'prediction' and 'expectation' when applied to cases such as the physical tuning of receptors to adaptively significant cues. I think in one sense this is wise – because there is a risk otherwise of debasing the whole PP programme into a restatement of the

principle of evolution: organisms are adapted to their environmental niche. However, in another sense it seems problematic for Clark's claim that PP is the perfect partner for the embodied mind. Clark, at some points seems keen to encompass examples of problems solved through embodiment (such as the passive dynamic walker (McGeer 1990)) and associated cheap processing tricks to argue that "rich knowledge based strategies and fast frugal solutions are merely different points on a single scale" (p.251) of PP. Yet at others he appears to introduce a dichotomy in which "bedrock adaptive states and responses" including inherited physical form and hardwired reflexes, are merely "setting the scene for the deployment (sometimes, in some animals) of more explicit prediction error minimizing strategies" (p.265) to add their magic.

Indeed, Clark seems to consider some invertebrates outside the scope of the unifying PP theory, suggesting (Clark 2013) "the humble earthworm" may not experience "perceptual touch (as opposed to mere causal contact) with a distal world" (p243-244). Should we say the same of crickets, bees, dragonflies and ants, perhaps on the basis that they lack a cortex? I hope that the above survey might bring philosophers to hesitate before condemning these animals also to fall outside the scope of cognitive science. Whether they can be considered examples of cognitive systems that operate without PP, or an example of convergent evolution to the PP solution, they provide an interesting light on the entire debate.

For example, this puts focus on whether cognitive adaptability is a diverse collection of neat tricks (of which PP is just one) or really is one, central, neat trick (PP). Indeed, as we start to flesh out the details of how PP is implemented in the brain, this distinction may start to dissolve: PP might be a necessary condition for a mind, but it is almost certainly not sufficient. This is aptly illustrated by the results of the recent DARPA challenge, in which many of the humanoid robots had the capacity to use sophisticated probabilistic generative models, but few were able to walk without falling over (Krotkov et al. 2017). In the end, understanding the physical interfaces and basic reflexes may still be essential, and insects can provide a gateway to unravelling how mechanisms of predictive processing become embedded in such systems to enrich the capacity for successful, intelligent action in the real world. We should continue to think about minds beyond the cortex.

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